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BRANCHIAL CIRCULATION IN *MACROPODUS OPERCULARIS* L.

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The purpose of this paper is to describe the adult vascular system of the branchial region in *Macropodus opercularis*, and to present some developmental details of this system starting with the free swimming larva.

Macropodus opercularis, the forked-tailed paradise fish, is listed by Jordan (1923) under the Order Labyrinthici, Family Osprohomenidae. This species is normally found in lowland streams and ponds of China and Formosa. The ability of the paradise fish to utilize atmospheric oxygen in addition to the normal gill respiration adapts it to life in stagnant waters.

The presence of the labyrinth structure in this fish and related species has led a number of investigators to study the nature of the accessory respiratory apparatus. Zograff (1888) and Day (1868) have shown that the labyrinth structure is used by the fish to retain air and not water as was originally believed. Henninger (1907), Das (1927), and Bader (1937) have shown that the labyrinth fish die when deprived of free access to atmospheric oxygen even if supplied with well oxygenated water. Bader (1937), confirming the work of Henninger (1907), has probably made the most detailed study of the blood system in the adult fish.

The present study dealing with the adult vascular system agrees with the description given by Bader (1937). The developmental details presented in this study add some details not found in the present literature.

MATERIALS AND METHODS

The species utilized in this study was *Macropodus opercularis*. Pairs were bred approximately every 4 weeks in controlled temperature tanks. The optimum temperature for breeding seemed to be between 27–30°C. Fish raised in the same tank from the same group of eggs show considerable variation in rates of growth. A range in size of from 5.0 mm. to 11.2 mm. 4 wk. after hatching represents an extreme example of variability in rates of growth. Subsequent studies of serial sections have shown little developmental difference between fish of the same size but of different age. For this reason, age groups were discarded in favor of measurement of length as a criterion for degree of development.

All fish measurements are based on standard length described by Hubbs (1943) that is, distance from the most anterior part of the head backward to the end of the vertebral column.

All fish were fixed in Bouin's fixative 6 to 24 hr. depending on the size of the fish. Serial paraffin sections were made of the head and body region of the fish. The sections were cut from 8 to 15 μ in thickness. The stains used were Delafield's hematoxylin and eosin, and Mallory's Triple Connective Tissue stain. Dioxane was used in place of the graded series of alcohols for dehydration purposes.

Photographic reconstructions (fig. 1) were made of the following stages, 2.9, 3.4, 4.3, 5.1, 7.4, and 11.2 mm.

OBSERVATIONS

A. 2.9, 3.4, and 4.3 mm. Stages

The general course and distribution of the afferent and efferent branchial arteries observed in these 3 stages were found to be similar. The 2.9 mm. fish represents the earliest free-swimming larval stage.

With a few minor exceptions the course and distribution of the afferent and efferent branchial arteries of these early stages are similar to the conditions found in Teleosts. (figs. 9, 10).

The efferent branchial artery IV although quite small was observed in the fourth branchial arch. Its junction with either the third efferent artery or the dorsal aorta was not found. It is possible that this junction does take place through small capillary vessels. The pair of efferent branchial arteries III one on each side, after passing through the branchial arches, were observed to join medially forming the dorsal aorta. Slightly anterior to the junction of the two efferent branchial arteries III, the dorsal aorta branches forming two lateral dorsal aortae. The efferent branchial arteries II and I join the lateral dorsal aortae. Anterior to the junction of the lateral dorsal aortae and the efferent arteries I, the lateral dorsal aortae continue anteriorly and seem to correspond functionally to the internal carotids. Just before its junction with the lateral dorsal aorta the first efferent branchial artery gives off a small branch which proceeds forward along the inner wall of the labyrinth groove, where it breaks up into capillaries.

The afferent branchial arteries observed in all stages of *Macropodus* were found to follow the same pattern commonly observed in Teleosts. The first and second afferent arteries arise independently from the ventral aorta, while the third and fourth pairs arise from the ventral aorta by means of a short common stem.

B. 5.1 mm. Stage

The development of the labyrinth groove which is to form the labyrinth organ of the adult fish is accompanied by some changes in the efferent branchial arteries (fig. 8). As in the earlier stages described, the third and fourth efferent branchial arteries join and empty into the dorsal aorta by means of a common trunk. Anterior to this common trunk the dorsal aorta branches forming the two lateral dorsal aortae. The second efferent branchial arteries from either side join the lateral dorsal aortae. Several changes in the efferent branchial system were observed.

1. The internal sacculus artery arises from the second efferent branchial artery just before it joins the lateral dorsal aorta. The internal sacculus artery continues anteriorly for a short distance before dividing into two branches. One branch continues forward and laterally toward the inner wall of the labyrinth groove where it breaks up into capillaries. The second branch was also observed to form a capillary network along the inner wall of the labyrinth groove.

2. The first efferent branchial artery instead of joining the lateral dorsal aorta continues anteriorly as the labyrinth artery. The labyrinth artery was traced as far as the anterior dorsal side of the labyrinth groove where it eventually breaks up into capillaries.

C. 7.4 and 11.2 mm. Stages

The vascular system of the branchial region observed in these two stages is substantially identical with the description given by Bader (1937). At these later stages the labyrinth organ is completely formed. A description of this organ is given by Bader (1937).

The third and fourth efferent branchial arteries unite to form a common trunk. The right and left common trunks unite forming the dorsal aorta. The common carotid arteries originate on either side from the efferent branchial artery III, just before its union with the efferent branchial artery IV. The common carotids after their origin proceed anteriorly for a distance before each divides into an internal and external carotid artery. The external carotid continues anteriorly along the inner wall of the labyrinth organ. The right and left internal carotids also proceed anteriorly and gradually converge. The two internal carotids pass between the pseudobranchs and unite just anterior to the pseudobranchs forming the circulus cephalicus (fig. 2).

The second efferent branchial artery does not join the dorsal aorta directly or indirectly through a lateral dorsal aorta. The second efferent branchial artery continues anteriorly as the internal sacculus artery along the inner wall of the labyrinth organ. Along its course the internal sacculus continues to subdivide forming a capillary network.

The first efferent branchial artery does not contribute directly or indirectly to the formation of the dorsal aorta. After leaving the gill arch the first efferent artery continues anteriorly along the labyrinth plate as the pabyrinth artery. Along its course the labyrinth artery continues to subdivide forming a network of arterial capillaries. The external sacculus artery originates from the first efferent branchial artery just before the first efferent artery continues anteriorly as the labyrinth artery. The external sacculus artery proceeds anteriorly along the outer wall of the labyrinth organ (fig. 4). This artery also subdivides and eventually forms a large capillary network along the outer wall of the labyrinth organ.

The blood from the head and labyrinth organ is returned to the heart by means of several large vessels. The labyrinth vein drains and collects blood from the inner wall of the labyrinth cavity. The blood from the inner wall of the labyrinth cavity, as well as the blood from the anterior and posterior portion of the cavity is collected by the two internal sacculus veins. (fig. 5.) The jugular vein drains the head region. The labyrinth vein, the external, and the two in-internal sacculus veins all empty into a large collecting sinus called by Bader (1937) the "Venoser sommelraum." (fig. 6) The blood is drained from this sinus into the jugular vein. The two jugular veins proceed posteriorly and empty the blood into the sinus venosus. (fig. 11).

The venous system draining and returning the blood from the head and body regions anterior to the heart is very much simplified in the early stages. From the 2.9 to 5.1 mm. stages, the only large veins observed were the jugular veins. The external and internal sacculus veins and the labyrinth veins found in the adult were not observed in the early stages.

DISCUSSION

The vascular system of the branchial region in the adult *Macropodus* deviates considerably in some respects from the pattern commonly found in Teleosts. It is quite possible that the development of the supplementary respiratory apparatus, the labyrinth organ, found in *Macropodus*, is a contributing cause of these deviations.

With some slight variations, all four efferent branchial arteries in Teleosts empty into the lateral dorsal aorta. In some instances as pointed out by Allis (1912), all four pairs empty independently into the lateral dorsal aorta, while in other instances, the first two pairs of efferent arteries empty independently into the lateral dorsal aorta and the third and fourth pairs first unite forming a short common stem. The pattern found in *Macropodus* is somewhat different. The first and second efferent arteries do not empty into the dorsal aorta, but proceed anteriorly as the labyrinth and internal sacculus arteries.

In Teleosts, as described by Allis (1912), the external carotid has its origin in the angle formed where the first efferent branchial artery joins the lateral dorsal aorta. After giving off its external carotid, the lateral dorsal aorta becomes the internal carotid. The common carotid is extremely short. In the adult *Macropodus* the common carotid is relatively long and originates from the third efferent branchial artery. The common carotid after its origin from the third efferent artery continues forward for some distance then divides into the external and internal carotids.

The venous system of the branchial region of the adult *Macropodus* also differs from the common Teleost pattern. The labyrinth vein, the external and two internal sacculus veins, and the large collecting sinus make up a relatively large venous system not found in Teleosts (fig. 11).

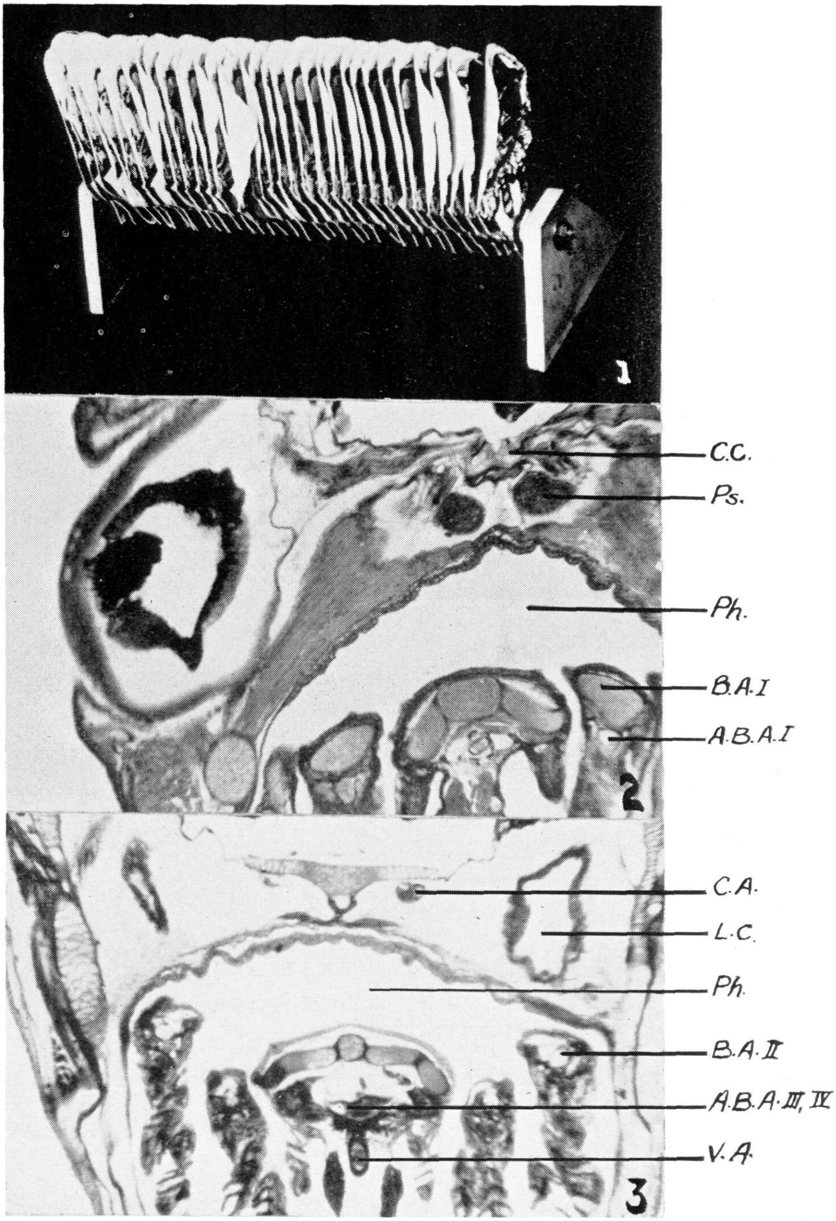
The study made of the various serial sections of *Macropodus* shows a gradual change in the vascular system of the branchial region. In the early stages, the 2.9 to 4.3 mm., the vascular system of the branchial region in *Macropodus* follows the general Teleost pattern. In the 5.1 mm. stage the first efferent branchial artery does not join the lateral dorsal aorta, but proceeds anteriorly as the labyrinth artery. The common carotid artery seems to be a continuation of the lateral dorsal aorta. In the 7.4 mm. stage neither the first nor the second efferent arteries join the dorsal aorta, the second efferent artery proceeding anteriorly as the internal sacculus artery. The common carotid originates from the third efferent branchial artery.

The study of the various serial sections seems to indicate that the changes in the branchial circulation of Macropodus occur gradually as the labyrinth organ develops.

For the sake of comparison, diagrammatic drawings of the branchial circulation are given in figures 7 to 10.

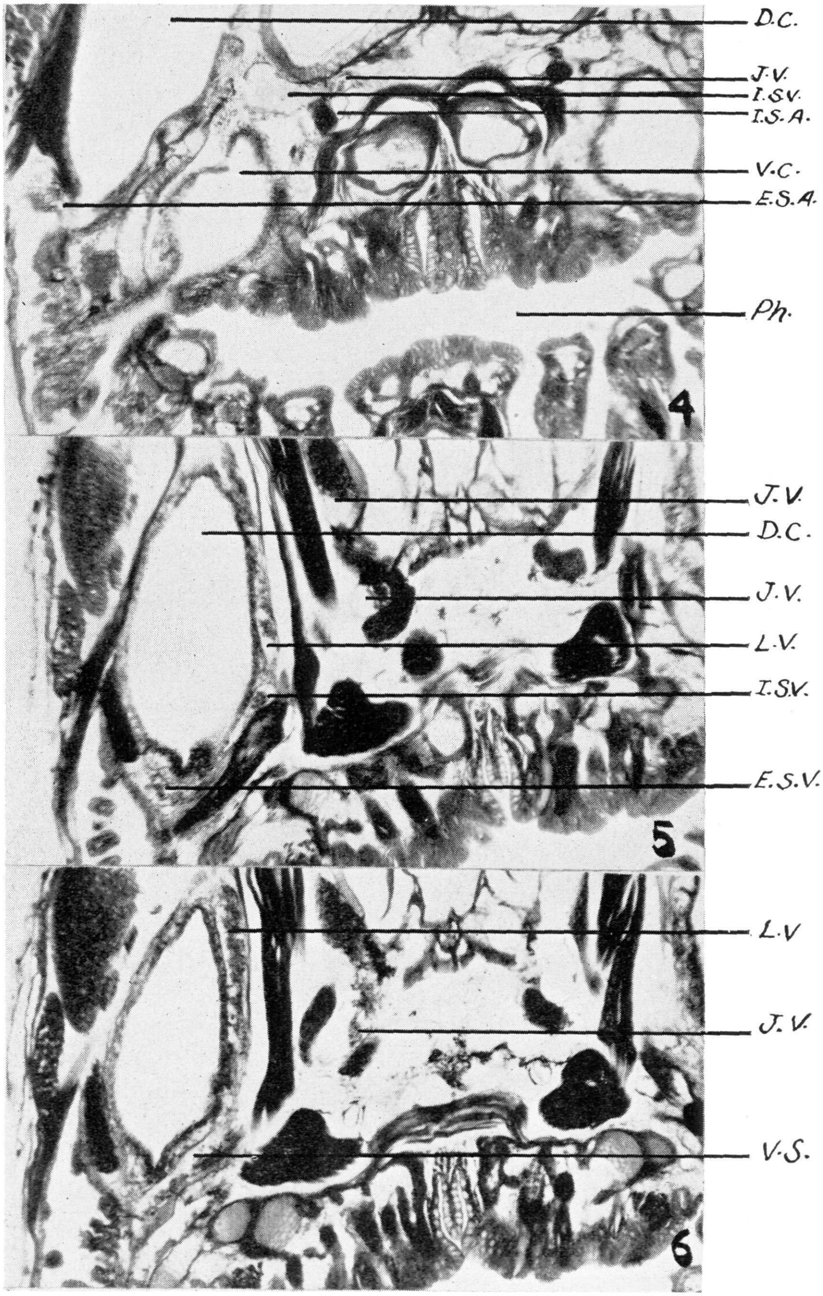
SUMMARY

1. Length rather than age of *Macropodus* is a more accurate criteria for determining the stage of development.
2. The vascular system of the branchial region in the early stages up to the 4.3 mm. stage in *Macropodus* is similar to the common Teleost pattern.
3. In the 5.1 mm. stage the first efferent branchial artery no longer empties into the lateral dorsal aorta but continues anteriorly as the labyrinth artery.
4. In the 7.4 mm. fish neither the first nor the second efferent arteries empty into the dorsal aorta. The second efferent artery continues anteriorly as the internal sacculus artery. The common carotids originate from the third efferent arteries.
5. The adult *Macropodus* possesses a relatively large and unique venous system in the branchial region consisting of the labyrinth vein, the external sacculus vein, and two internal sacculus veins draining blood from the labyrinth organ.
6. Observations show that the deviations from the common Teleost pattern occur as the accessory respiratory apparatus, the labyrinth organ, develops.



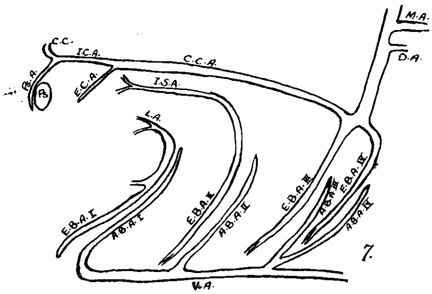
1. Photographic reconstruction used to study the circulatory system.
2. Transverse section of an 11.2 mm juvenile fish through the pseudobranchs and through the posterior part of the eye. X93.
3. Transverse section of a 7.4 mm. fish showing the common stem formed by the 3rd and 4th efferent branchial arteries. X 93.

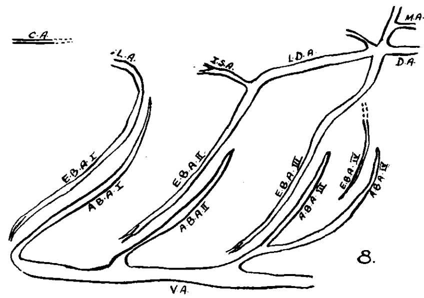
(See page 135 for Abbreviation Key)

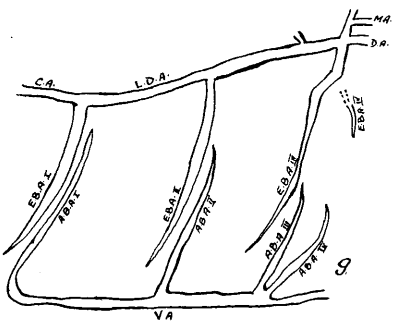


4. Transverse section of an 11.2 mm. fish through the labyrinth chambers. X93.
5. Transverse section of an 11.2 mm. fish through the posterior portion of the labyrinth chambers. X93.
6. Transverse section of the same fish showing the venous collecting sinus—"Venoser sammelraum". X93.

(See page 135 for Abbreviation Key)







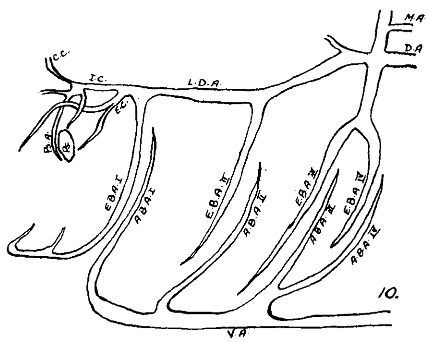


FIGURE 7. Lateral view of the branchial arteries of the adult *Macropodus* shown diagramatically.
FIGURE 8. Similar view of a 5.1 mm. *Macropodus*.
FIGURE 9. Similar view of early stages up to 5.1 mm. in *Macropodus*.
FIGURE 10. Similar view of Teleost system. Adapted from Allis (1912).

ABBREVIATION KEY

A.B.A.	Afferent branchial artery
B.A.	Branchial arch
C.A.	Carotid artery
C.C.	Circulus cephalicus
C.C.A.	Common carotid artery
D.A.	Dorsal aorta
D.C.	Dorsal chamber of labyrinth chamber
E.B.A.	Efferent branchial artery
E.C.A.	External carotid artery
E.S.A.	External sacculus artery
E.S.V.	External sacculus vein
I.C.A.	Internal carotid artery
I.S.A.	Internal sacculus artery
I.S.V.	Internal sacculus vein
J. V.	Jugular vein
L.A.	Labyrinth artery
L. C.	Labyrinth chamber
L.D.A.	Lateral dorsal aorta
L.V.	Labyrinth vein
M.A.	Mesentary artery
Ph.	Pharynx
Ps.	Pseudobranch
Ps.A.	Pseudobranchial artery
V.A.	Ventral aorta
V.C.	Ventral chamber of labyrinth chamber
V.S.	Venoser sammelraum

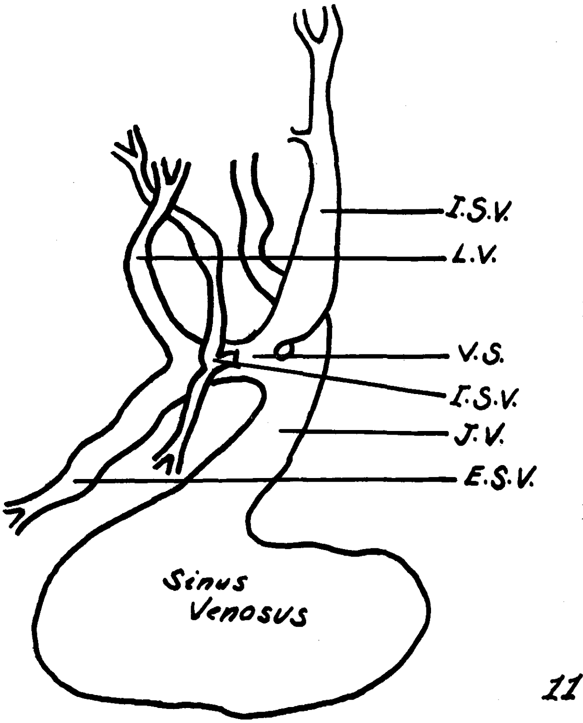
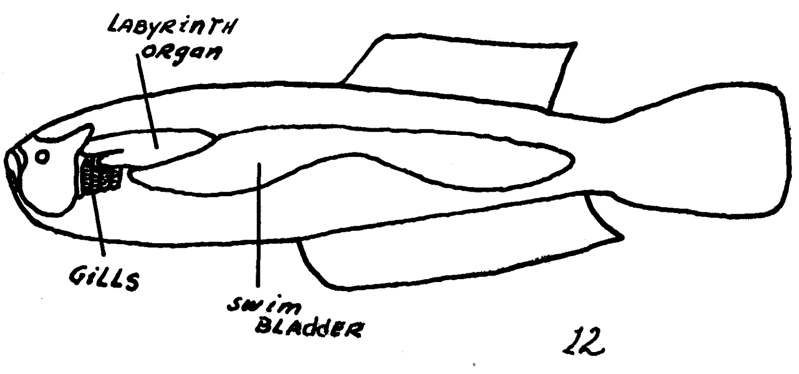


FIGURE 11. Reconstruction after Bader (1937) showing the veins associated with draining the labyrinth organ.

FIGURE 12. The labyrinth organ in relation to the general morphology of the head and branchial region. Adapted from Bronns (1940).



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